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MEASURE OF THE SPACING BETWEEN INDIVIDUALS WITHIN A POPULATION

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INTRODUCTION

SPACING in nature between individual organisms of a given species is of great ecologic significance. The tendency of individuals to occur singly or in aggregations affects the degree of utilization of the local habitat. The spacing of the individuals within a community, furthermore, affects all those social or ecologic interrelations that may exist at any given time among the individuals of the same or of differing species. Methods for describing accurately the spacing of the individuals are consequently needed in any consideration of the organization either of societies or of communities.

Methods for measuring the spacing between individual plants have been proposed by several ecologists (Raunkiaer, 1934; Cottam and Curtis, 1949). Unfortunately, none of the proposed methods provides for the statistical treatment of the measurements, and they have other deficiencies as well.

Since a practical method for the direct measure of the spacing between the individuals making up a population is lacking, their pattern of distribution has in the past been deduced mostly from counts of the number of individuals on sample plots taken at random. If the individuals are distributed over an area at random, the number of sample

plots containing 0, 1, 2, 3, and so on, individuals should fall into a Poisson series. Inasmuch as the variance of a Poisson series is equal to the mean of the series, a comparison between the variance and the mean of the samples gives information about the type of distribution of the individuals. A variance that is less than the mean indicates a spacing of individuals that is more uniform than random, while a variance that is larger than the mean indicates a tendency of the individuals to occur in clumps or groups (Fisher, 1915; Beall, 1935; Clapham, 1936).

The variance/mean ratio gives a rough indication of whether or not the distribution of a species in a particular series of samples is random, but no satisfactory mathematical procedure is available for measuring the significance of the divergence of any particular variance/mean ratio from that expected in a random distribution, nor for comparing the differences between the distribution patterns of two or more series of samples (Cole, 1946). A large number of plots must be sampled in order to secure a reliable basis for calculation. The results also are seriously affected by the population densities and by the sizes of the sample plots employed (Evans, 1952). Furthermore and of utmost importance, no direct measure is obtained by the sample-plot method of the actual distances between the individuals.

In order to overcome these difficulties I have for several years been experimenting with methods for measuring directly the spacing of the individuals in a community. In the following sections I shall describe the method that has proved most efficient for this purpose and shall present several examples of its application to concrete cases.

The populations of plants whose spacing is here described are on the Edwin S. George Reserve of the University of Michigan, Livingston County, Michigan (Evans and Cain, 1952). Measurements of the spacing of three of the species, *Solidago rigida* (goldenrod), *Lespedeza capitata* (bush clover), and *Liatris aspera* (blazing star), have been made on a large chart constructed by Cain and Evans (1952) of the distribution of these plants over a grassy plot covering 7873 square meters. The spacing of *Hieracium longipilum* (hawkweed) was measured directly in the field on a grassy plot covering 267 square meters. The spacing of the forest trees was also measured in the field on a plot covering 6856 square meters.

Acknowledgments

For assistance in taking measurements in the field of the spacing between individual plants I am indebted to Elizabeth Dice, Francis C. Evans, and John A. King. Stanley A. Cain and Francis C. Evans (1952) have kindly allowed the use of their large chart on which the distribution of three species of plants had been plotted. Measurements of the distances between the plants on this chart were made by William B. McIntosh and William Prychodko, who also made most of the statistical computations here presented. John A. King made the plot of random dots used in a part of the study. George W. Thomson has given valuable advice on statistical methods.

METHOD FOR MEASURING SPACING BETWEEN INDIVIDUALS

In order to obtain a basis for the calculation of means and of the variability of spacing between individuals within populations it is necessary to adopt a standard procedure for taking the measurements. After a considerable amount of experiment with various procedures, I propose the following method:

1. The necessary number of individuals to be taken as points of origin for the measurements are located by some process of random sampling.

2. From the center of each individual which is taken as a point of origin the distance is measured to the nearest other individual of the same kind in each of the 6 surrounding sextants (Fig. 1). From each point of origin 6 independent measurements of spacing are consequently obtained.

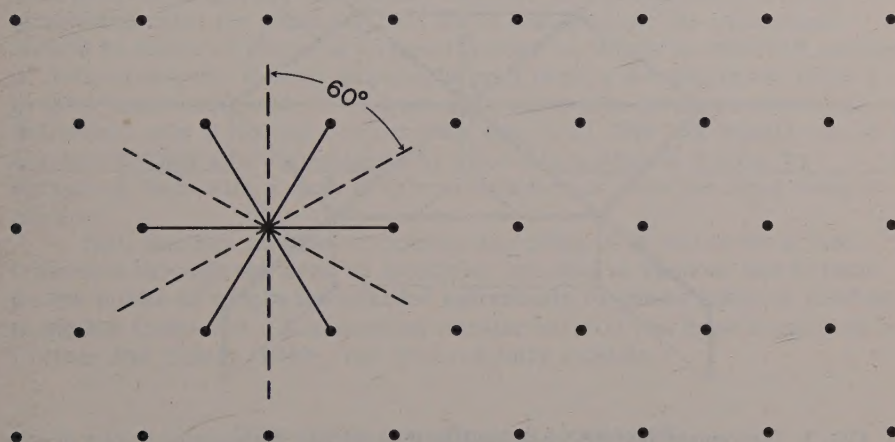


FIG. 1. Method proposed for measurement of spacing between individuals which are evenly spaced over a plane surface. From any individual taken as a point of origin, the distance is measured to the nearest adjacent individual in each of the surrounding sextants (marked by broken lines).

3. The measurements of the distances between individuals obtained by this procedure may then be treated by the statistical methods to be described in a later section of this paper.

Instruments

For laying out the sextants around each point of origin a surveyor's transit or a sighting compass may be used. One procedure is to set a compass on a tripod centered exactly over the individual which forms the point of origin. Assume that a magnetic south-north line forms the

western boundary of the first sextant. Now rotate the sights 60 degrees clockwise to locate the other boundary of this first sextant. Measurement is then made with a steel tape or rule to the nearest adjacent individual within this sextant. The compass sights are then rotated another 60 degrees further clockwise to delimit the next sextant, and so on.

A special instrument with 6 equally spaced arms radiating outward from a common center greatly facilitates the taking of the measurements. The space between any 2 arms forms a sextant. The device which I have constructed (Fig. 2) is made of heavy brass and has sufficient weight not to be easily displaced while the measurements are

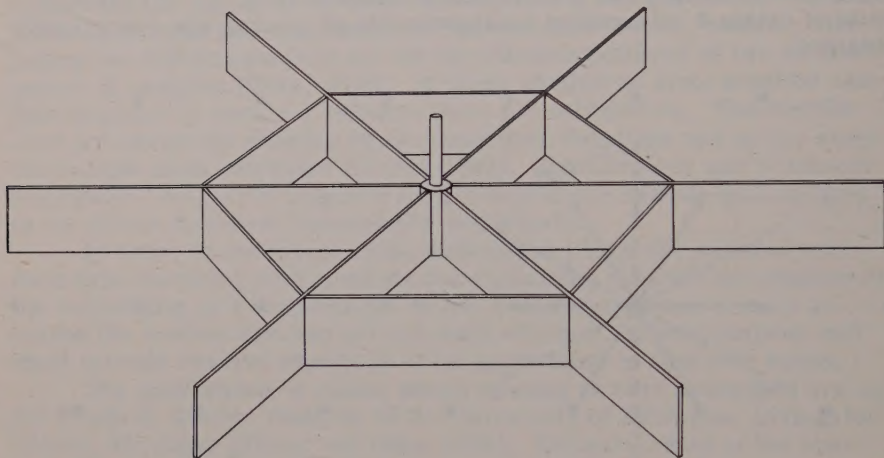


FIG. 2. Instrument devised for delimiting the sextants surrounding a point of origin. To a central cylinder of brass $\frac{3}{4}$ inch in diameter, 6 equally spaced arms are soldered. Each arm is made of a strip of brass $\frac{1}{8}$ by $1\frac{1}{2}$ by 12 inches. Braces between the arms midway of their lengths enforce rigidity for the device. The central cylinder is tapped above to receive a $\frac{1}{4}$ -inch brass pin and below to receive a camera-tripod screw.

being made. The center of the instrument is placed directly over the individual chosen to be the center of origin for the measurements. The instrument may either be placed directly on the ground, in which case it will crush any delicate plant somewhat, or it may be supported on a tripod. A magnetic compass is used to orient 1 arm of the instrument to point north. One end of a steel tape is next fastened to the center pin of the instrument, so that its zero reading is exactly in the center of measurement. A single observer can now locate the sextants by sighting along the arms and also can measure directly the distance to the nearest plant in each sextant. An assistant to record the measurements as they are taken, however, will expedite the field work.

Random Sampling

For selecting the individual organisms which are to be used as centers of origin for the measurements of spacing, some method of random sampling must be used. If the total number of individual organisms on the plot to be sampled is not very great, each of them may be numbered serially. Small cardboard price tags, each with a string attached, are satisfactory for this purpose. Before going into the field the tags should be numbered serially and placed in order on a wire loop. From a table of random numbers the points of origin are then drawn. If, for example, approximately 300 measurements are desired, then 50 points of origin may be drawn.

A less laborious method is to begin at 1 edge of the plot to be covered and as each individual organism is encountered to make a random drawing to ascertain whether or not this individual is to be taken as a point of origin for the measurements. If a preliminary survey should indicate, for example, that about one-tenth of the individuals should be taken as points of origin in order to obtain the desired number of measurements, then by drawing a card from a set numbered from 1 to 10 as each individual is encountered, one would measure from that individual only if the card drawn was, say, a 9. The individuals can be marked as they are encountered by attaching a wisp of cotton, by splashing them with a dash of talcum powder, or in some other simple manner.

Still another method of random sampling is to run several line transects through the area at locations selected at random and to take as the points of origin the nearest individuals to points taken at random along the transects. A somewhat similar method has been suggested by Cottam and Curtis (1949), but it is not fully random.

Difficulties Sometimes Encountered

Sometimes it is difficult to locate the precise middle of an individual which is to serve as a point of origin or as an end point for the measurements of spacing. For most plants it will be best to take as the point of measurement the middle of the main stem where this emerges from the ground. If there is no main stem, but instead only a group of stems, then the middle point among the stems will serve as the point of measurement.

It will be impossible to measure the spacing of active mobile animals, except as these may be located at some fixed instant of time, as might be true if they were photographed from above. In such case the point of origin of the measurements could either be taken to be the middle of the main part of the body or of the head. So long as the method of taking the measurement is clearly stated and the observer is consistent in his procedure, it should make little difference what point of origin is taken. For those sessile animals which lack a clearly defined head, the middle of the body can be taken as the point of origin for the measurements.

Where the point of origin is a tree or bush over which the sighting compass or other instrument cannot be set up, the position of the compass used to locate the sextants can be shifted a specified distance to the right or to the left. Allowance for this shift must then be made when ascertaining which is the nearest other individual in each sextant, always keeping in mind that the sextant under consideration surrounds the actual point of origin and not the shifted position occupied by the compass. The actual measurements of spacing will of course be made directly from the point of origin to the nearest individual in each sextant.

Frequently, when taking measurements of spacing, no individual of the appropriate kind is encountered within a particular sextant until the boundary of the plot under study is reached. If the plot is surrounded by habitat of essentially the same character as that within the plot, then I see no objection to measuring to the nearest individual within the sextant concerned, irrespective of whether that individual is inside or outside of the artificial boundaries of the plot. On the other hand, if the type of habitat changes, either within or outside the plot, in a way that might affect the distribution of the individuals in a particular sextant, then that sextant should be omitted from consideration. It may consequently happen that fewer than 6 measurements of spacing may be obtained from some points of origin.

The reduction in number of measurements from any point of origin below 6, by reason of failure of occurrence of any individual of the species under consideration in the sextant concerned until the boundary of the plot is reached, will tend to depress the calculated mean of the spacing between individuals. This is true because the omission usually will indicate a more than average gap between individuals in that direction. One should consequently strive to avoid such incomplete measurements. One way to accomplish this is to omit as points of origin any individuals which happen to lie closer to a boundary of the plot than some previously chosen distance, say about twice the expected mean distance between individuals.

Should 2 points of origin lie close together, it may happen that the distance between these 2 individuals will be represented in 2 sets of sextant measurements. Inasmuch as such duplicated measurements will occur most frequently between closely adjacent individuals, the inclusion of duplicate measurements in the calculation of a mean will tend toward an erroneous lowering of its value. Only 1 measurement between any 2 points should consequently be included in the calculations and all duplicate measurements should be discarded.

Items to be Treated as Individuals

In the measurement of the spacing in any population, careful definition must be made of the items which are to be treated as individuals. It must be clearly stated, for example, whether all individuals of a given species, irrespective of size, sex, or age class, have been considered or whether the spacing between individuals belonging only to certain classes has been measured. Individuals belonging to different species

can be considered to be members of the same population for the purpose of measuring their spacing. For example, we can measure the spacing of forest trees, irrespective of their species.

STATISTICAL TREATMENT OF MEASUREMENTS OF SPACING

The site which each individual organism occupies in its habitat covers a certain amount of space. When any individual is taken as a point of origin for measuring spacing, the number of possible sites for other individuals of the same species increases as the square of the distance from the point of origin. In treating statistically the measurements of spacing between individuals, consequently, the square-root transformation of the measurements will be appropriate. Means, variances, standard deviations, standard errors, and other similar statistics, therefore, may be calculated from the square roots of the measurements of the spacing between individuals taken according to the method described in the previous section.

The variability of the measurements of spacing may be measured by variance, standard deviation, or coefficient of variation in the usual fashion. When, however, the frequency curve of the measurements of spacing is skewed, as is true for many natural populations, then the variance and the statistics calculated from it may not give a fully reliable measure of variability.

RELATION OF TYPE OF DISTRIBUTION TO SPACING BETWEEN INDIVIDUALS

The distances that separate the individuals within any population are affected by their type of distribution. When the individuals are evenly distributed the measurements of the distances between them will have little if any variability. Should the individuals be irregularly distributed over the habitat the measurements of their spacing may be highly variable.

Uniform Distribution

Let us first consider a population in which the individuals are equally spaced over a plane. For such a distribution the maximum population density per unit of area will be obtained when the individuals are distributed in a triangular pattern (Fig. 1). In such a distribution any given individual is equally distant from the 6 nearest adjacent individuals (Cottam and Curtis, 1949). If one selects any particular individual as a point of origin and measures the distance to the nearest adjacent individual in each of the 6 surrounding sextants, 6 identical measurements will be obtained.

The reason for measuring to the nearest individual in each sextant surrounding the point of origin will now be evident. By so doing one ob-

tains a variance of zero under conditions of even spacing between individuals. Any departure from uniform distribution will be indicated, therefore, by the variance. A tendency toward even spacing, moreover, will produce a frequency curve of the square roots of the measurements of spacing which will be skewed to the right. The g_1 statistic of such a curve will have a negative value.

An approach toward uniform spacing is likely to occur in any population where there is severe competition between the individuals for sunlight, moisture, or some other essential factor which is present in limited supply. Animals that maintain territories, for example, tend to be distributed more evenly than random.

As an illustration of spacing that tends to be more regular than random, Figure 3 shows the frequency polygon for the square roots of the measurements of the spacing of forest trees within a certain grove. The trees considered in these measurements are only those which are of sufficient height to have become part of the forest canopy. Forest trees are in strong competition for sunlight and consequently they tend to be spaced at more regular intervals than random. In accordance with this expectation we find the frequency polygon of the measurements of the spacing of these trees to be skewed to the right. The amount of the skewness, as measured by g_1 , is -0.27 , which has a t value slightly below the 5 per cent level of significance (Table I). The g_2 measure of kurtosis is

TABLE I

Square Roots of Measurements (by Sextants) of Spacing Between Individual Plants of Certain Species Growing on the Edwin S. George Reserve, Livingston County, Michigan; also of Dots Distributed at Random Over a Plane Surface

Plant	Number of Measurements	Square Roots of Measurements of Spacing					
		Mean $\sqrt{\text{cm}}$	Standard Deviation	g_1	t_1	g_2	t_2
Hieracium ...	294	$8.09 \pm .20$	3.52	.96	6.75		
Lespedeza ...	274	$12.63 \pm .48$	7.96	2.25	15.30		
Liatris	430	$17.26 \pm .51$	10.73	1.14	9.74		
Solidago	251	$17.96 \pm .50$	7.87	.84	5.46		
Forest trees .	300	$21.39 \pm .28$	4.79	-.27	-1.92	-.04	-.14
Solidago → Liatris ...	246	$28.70 \pm .70$	10.90	.02	.14	-.59	-1.90
Liatris → Solidago...	248	$27.30 \pm .59$	9.29	.06	.39	-.49	-1.59
Random dots .	294	$\sqrt{\text{unit}}$ $2.22 \pm .04$	.64	.11	.77	-.50	-1.76

-0.04, which is insignificant. The forest measured was young, however, and was composed mostly of second-growth oaks and hickories. A more mature forest might be expected to be still more regularly distributed and to have a still greater negative value of g_1 .

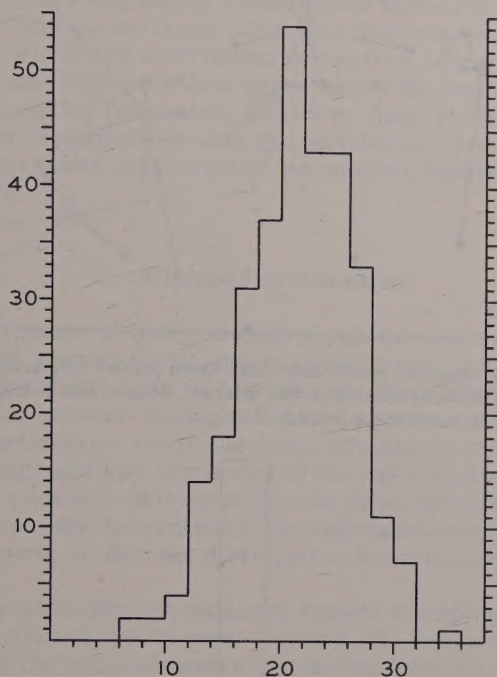


FIG. 3. Frequency polygon for the square roots of the measurements by sextants between those forest trees which extend into the forest crown in an oak-hickory grove on the Edwin S. George Reserve, Livingston County, Michigan.

Random Distribution

In order to measure the spacing in a population of individuals distributed at random over a plane surface a population of dots was placed on a sheet of cross-section paper. Each vertical and horizontal line on the paper was numbered and the positions of 500 dots were located by drawing from a table of random numbers. Fifty of these randomly distributed dots were drawn at random as points of origin for the measurements of spacing. From these points of origin, the distance to the nearest other dot in each surrounding sextant was measured, in accordance with the method previously described (Fig. 4). The frequency polygon for the square roots of these measurements is presented in Figure 5.

Owing to the method of placing the dots on the sheet of cross-section paper, no dots were closer together than 1.0 unit, and consequently the frequency curve of the square roots of the measurements of the spacing between dots is truncated at its lower end. Aside from this

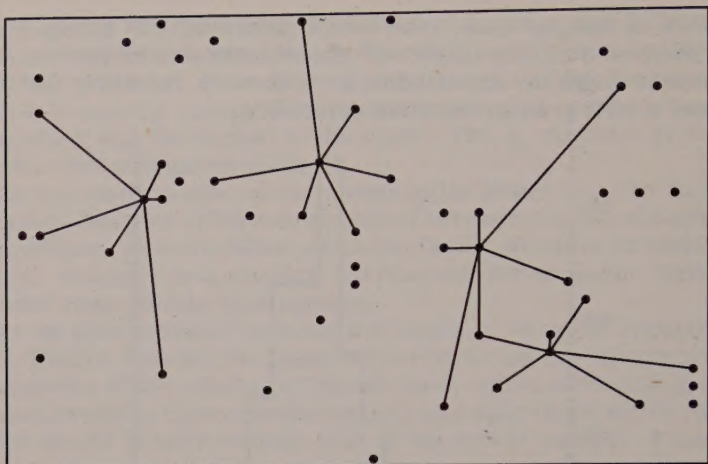


FIG. 4. Part of a sheet on which dots have been placed at random. It illustrates the method of taking measurements to the nearest dots in the sextants surrounding each of 4 dots taken at random as points of origin.

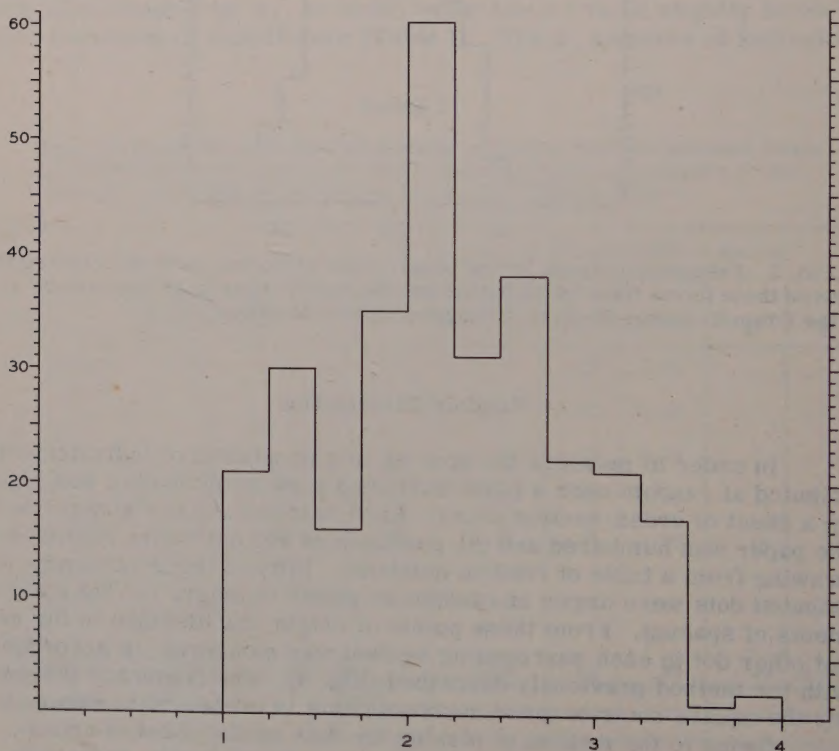


FIG. 5. Frequency polygon of square roots of spacing by sextants between 500 dots distributed at random over a sheet of cross-section paper, 100 x 100 units in area. Fifty dots were taken at random as points of origin for the measurements, which were by sextants. Incomplete and duplicate measurements not included.

discrepancy, the frequency polygon seems not to depart seriously from a normal curve. There is a negligible amount of skewness, as shown by a g_1 of 0.11. The small amount of kurtosis ($g_2 = -0.50$, $t_2 = -1.76$) is probably caused by the truncation of the lower end of the frequency curve. George W. Thomson has kindly recalculated these measures of the spacing of random dots on the assumption that they constitute a truncated sample from a randomly distributed population, using the method of Cohen (1950), and finds excellent agreement with expectation for a normal curve. It may be concluded, therefore, that the frequencies of the square roots of the distances between individuals of a randomly distributed population, when measured by the method described above, approach a normal curve.

Clumped Distribution

The individuals of many natural populations are distributed in more or less compact aggregations. Such aggregations may be produced by a tendency of the individuals to remain near their site of origin, by social attraction between the individuals, by the accumulation of the individuals in particularly favorable local situations, or perhaps by other causes. The aggregations composed of the individuals of certain species may be tightly clumped, leaving extensive unoccupied spaces between the aggregations. On the contrary, the aggregations of other species may be very loose, so that the distribution departs only slightly from random.

When any considerable tendency toward clumping is present in a population distributed over a plane surface, the frequency curve of the square roots of the measurements of spacing between the individuals, taken according to the method here proposed, will be skewed toward the left. This is illustrated in Figures 6 to 9, which are based on measurements of the spacing of the individuals of 4 species of plants.

The significance of the skewness of a frequency curve can be evaluated from g_1 , which is calculated from the third moments of the deviations from the mean. From Table I it will be seen that *Lespedeza* has the highest g_1 value (2.25), *Liatris* (1.14) is next, then *Hieracium* (0.96), while *Solidago* (0.84) has the lowest g_1 value of the 4 plant species whose distributional patterns are here compared. The departure of each of these species of plants from a random distribution, as measured by t , is highly significant. All of these plants are noticeably clumped in nature. *Solidago* is less strongly clumped than *Liatris* and *Lespedeza* is more strongly clumped than either of these 2 species (Thomson, 1952). For these 3 species, therefore, the magnitudes of the g_1 values of their measurements of spacing fall in the same order as their degree of clumping. I have no estimate of the degree of clumping in the field of *Hieracium*, as compared to that of the other 3 species of plants. I conclude that the g_1 statistic is useful for measuring the significance of the departure of any distribution from randomness and that it may also give a rough measure of the strength of clumping.

Any attempt to specify the type of distribution of an irregularly spaced population by a single statistic, however, seems likely to be

futile. The spacing of individuals in a population exhibits many diverse types of irregularities. The spacing of the individuals within each aggregation may be uniform, random, or irregular. The density of the aggregations may vary from compact to loose. The boundaries of the several

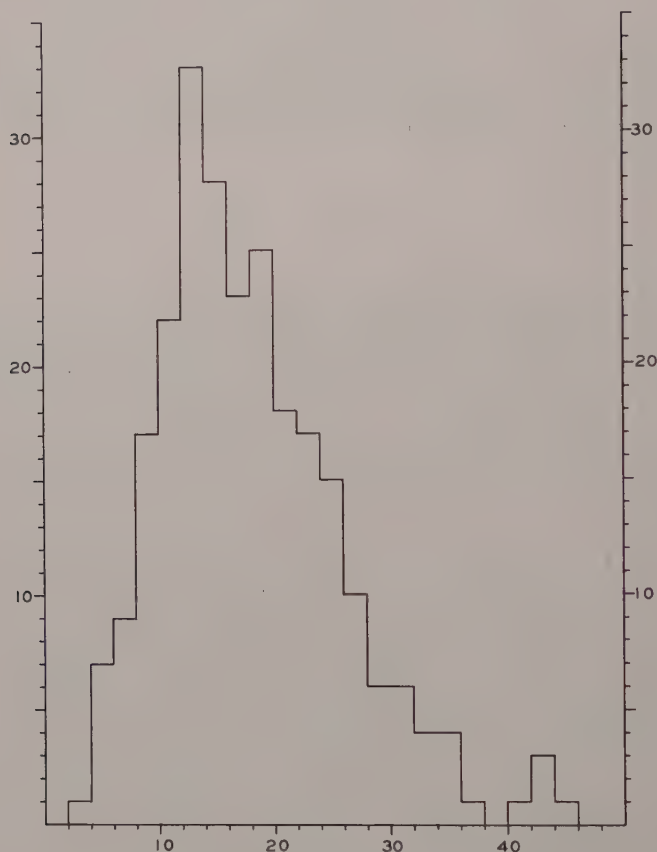


FIG. 6. Frequency polygon for the square roots of the spacing between individuals of *Solidago rigida* on a grassy area on the Edwin S. George Reserve, Livingston County, Michigan, as plotted by Cain and Evans (1952). Measurements taken by sextants. Incomplete and duplicate measurements omitted.

aggregations may vary from sharp to indistinct. The aggregations themselves also may be distributed evenly, at random, or very irregularly. Furthermore, there may be various degrees of secondary or even tertiary clumping within the major aggregations. Measures of skewness and of kurtosis will often assist in the analysis of distribution, but such statistics cannot be expected to give a complete description of the organization of a complex population.

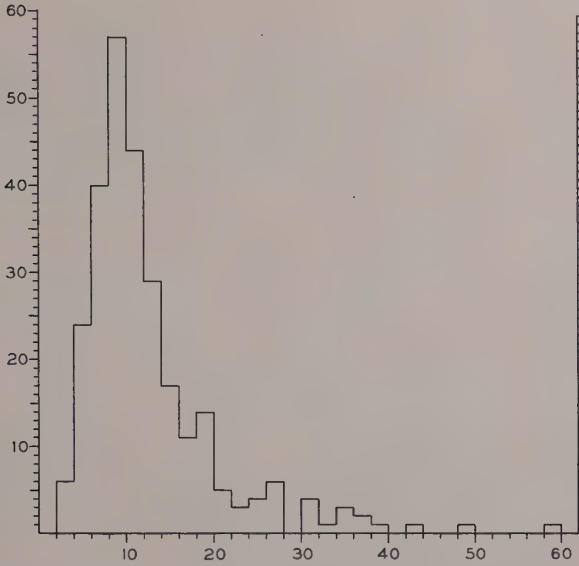


FIG. 7. Frequency polygon for the square roots of the spacing between individuals of *Lespedeza capitata* on a grassy area on the Edwin S. George Reserve, Livingston County, Michigan, as plotted by Cain and Evans (1952). Measurements taken by sextants. Incomplete and duplicate measurements omitted.

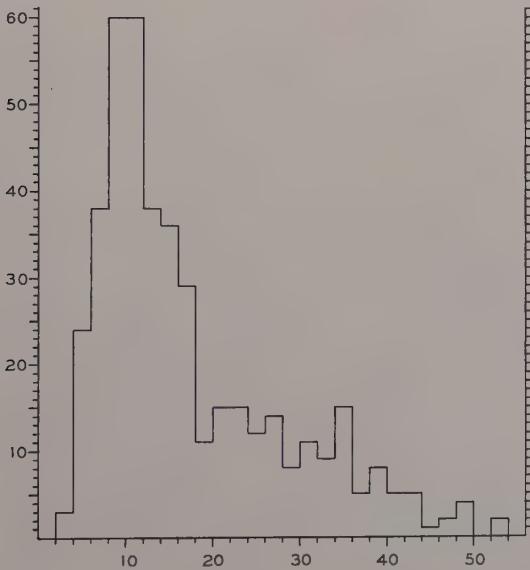


FIG. 8. Frequency polygon for the square roots of the spacing between individuals of *Liatris aspera* on a grassy area on the Edwin S. George Reserve, Livingston County, Michigan, as plotted by Cain and Evans (1952). Measurements taken by sextants. Incomplete and duplicate measurements omitted.

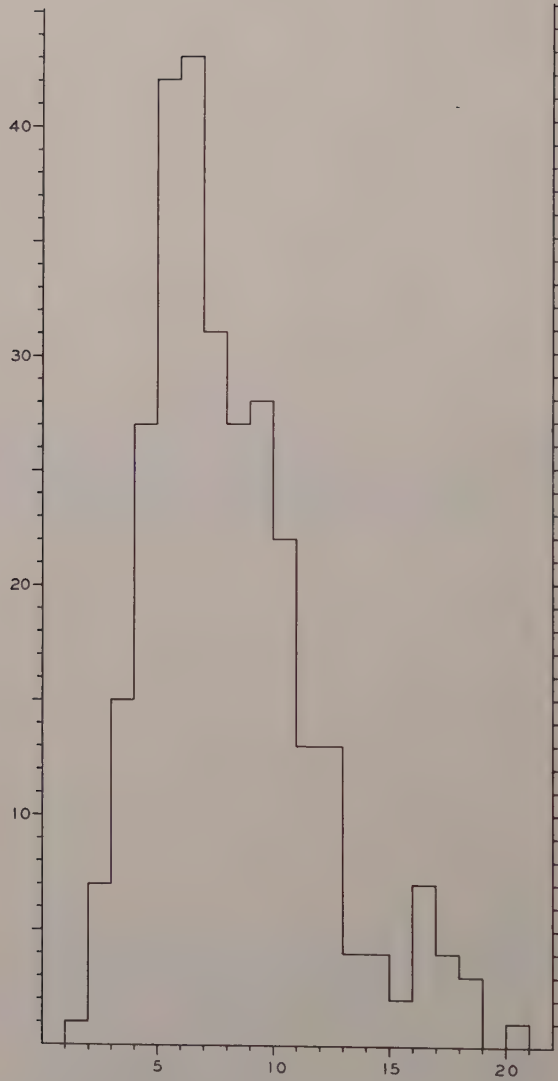


FIG. 9. Frequency polygon for the square roots of the spacing between individuals of *Hieracium longipilum* on a grassy plot on the Edwin S. George Reserve, Livingston County, Michigan. Measurements taken by sextants. Incomplete and duplicate measurements omitted.

When the individuals of a population occur in compact clumps with completely unoccupied spaces separating the clumps, then the measurements of spacing between the individuals will form a bimodal curve. That this must be so is demonstrated in Figure 10, in which a hypothetical population of dots is distributed in clumps of 7, the individual dots within the clumps and the clumps themselves being evenly spaced

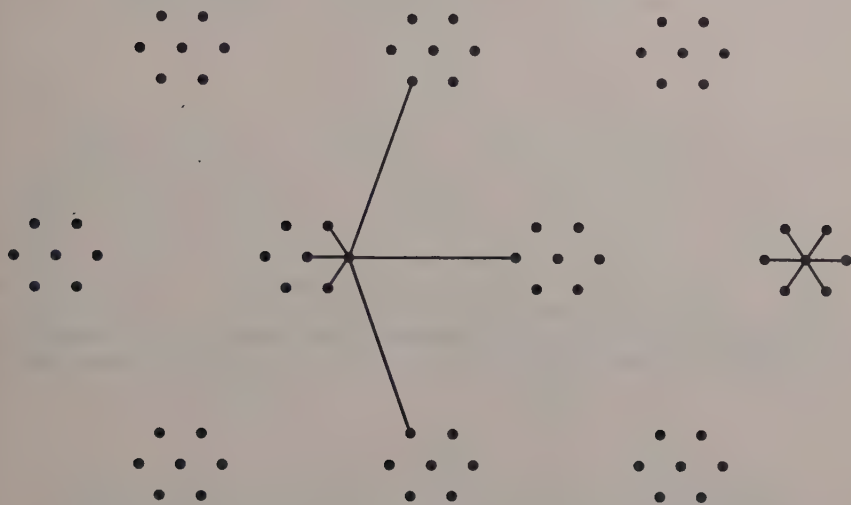


FIG. 10. Measurements of spacing by sextants from individuals in a population of dots, which are distributed uniformly in clumps of 7, with the clumps evenly spaced apart.

apart. If the middle individual in any clump is taken as a point of origin, all the measurements of spacing, taken by sextants according to the method here proposed, will be equal. On the other hand, if an individual at the edge of a clump is taken as the point of origin, the measurements of spacing will be of 2 types, those to other individuals within the same clump, and those to the nearest individuals in adjacent clumps. The square roots of such measurements will form a bimodal curve, one mode representing the square roots of the spacing of the individuals within the clumps, the other mode representing the square roots of the spacing between the outside individuals of adjacent clumps.

In nature such a simple type of clumped distribution will never be encountered. The distances between clumps is certain to be variable, as well as the spacing of the individuals within the clumps. It will usually be more practical in the field to measure directly the spacing between clumps, rather than to estimate such spacing from measurements between individuals. Nevertheless, whenever a bimodal curve of the spacing within a population is encountered, it will indicate a tendency of the individuals to occur in compact and discrete clumps.

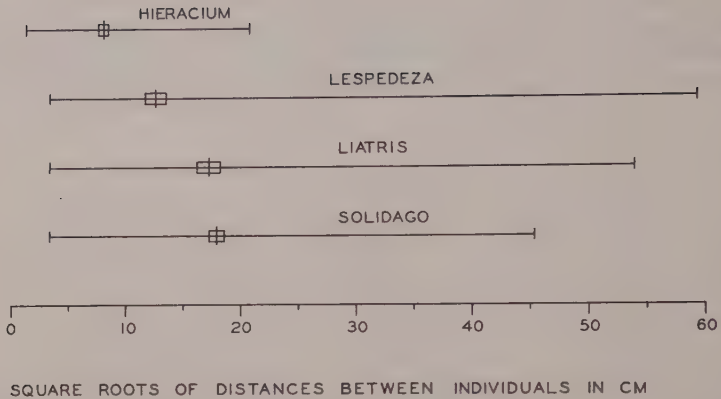


FIG. 11. Comparison between the spacing of 4 species of herbs on the Edwin S. George Reserve, Livingston County, Michigan, according to the method of Dice and Leraas (1936). For each species the length of the line gives the extremes of the square roots of the measurements, the heavy cross bar indicates the mean, the rectangle extends twice the standard error on each side of the mean.

Distribution in Three-dimensional Space

The spacing between individuals distributed in 3-dimensional space could be measured in somewhat the same manner as between individuals all of which lie on a single plane. It should thus be possible to measure the spacing between individual plants or animals that occupy different strata in a community. The making of measurements in 3-dimensional space, however, and the statistical treatment of such measurements would require special procedures which will not be considered in this paper.

COMPARISON OF SPACING IN DIFFERENT POPULATIONS

The means of the square roots of the spacing between the individuals in any 2 populations may be compared by the usual statistical method, which employs the standard error of the mean and its *t* value. Even though the 2 frequency curves may be skewed, their standard errors nevertheless are usually reliable as a basis for testing significance. In Figure 11 is presented a graphic comparison of the mean spacing of the 4 species of plants measured on the George Reserve. It is evident from this figure that *Hieracium* has a significantly lesser mean distance between individuals than any of the other species. The spacing of *Liatris* does not differ significantly from that of *Solidago*, but the average spacing between the individuals of both these species is significantly greater than that between the individuals of *Lespedeza*.

RELATIONSHIP BETWEEN SPACING AND POPULATION DENSITY

The density of a population in which the individuals are uniformly spaced and as densely packed as possible (Fig. 3) is inversely related to the square of the distance between individuals. In such a triangular distribution each individual occupies 0.866 of a square unit of the distance between individuals. Expressed in another way, there are 1.155 individuals per square unit. If we let S be the average distance in any standard units between the adjacent individuals of such a population and let P be the average population density per square unit of measurement, then:

$$P = 1.155/S^2, \text{ and } S = \sqrt{1.155/P} .$$

These formulas seem also to be applicable to populations which are distributed at random. For example, on the sheet of cross-section paper 100 x 100 units square, on which 500 dots were placed at random, as described above, the density of the dots was 0.05 per square unit. The mean spacing between dots should, therefore, be:

$$S = \sqrt{1.155/0.05} = \sqrt{23.100} = 4.806 .$$

The square root of the expected mean spacing between dots is 2.19. The actual mean of the square roots of the measurements of spacing between dots, taken by sextants, is 2.22 ± .04 (Table II), which does not differ

TABLE II

Comparison Between Calculated and Measured Spacing (by Sextants) in Populations Having Various Types of Distribution and with Dots Distributed at Random.

Plant	Mean Density Per m ²	Square Roots of Mean Spacing				Calculated Minus Measured √cm
		Calculated from Density √cm	Actual Measurements √cm g ₁ g ₂			
Hieracium	1.765	8.99	8.09 ± .20	.96	...	.90
Lespedeza	.108	18.10	12.63 ± .48	2.25	...	5.47
Liatris	.041	22.98	17.26 ± .51	1.14	...	5.72
Solidago	.064	20.61	17.96 ± .50	.84	...	2.65
Forest trees ...	.064	20.59	21.39 ± .28	-.27	-.04	-.80
Solidago → Liatris	.042	22.96	28.70 ± .70	.02	-.59	-5.74
Liatris → Solidago	.064	20.60	27.30 ± .59	.06	-.49	-6.70
	Per unit ²	√units	√units			√units
Random dots ...	.050	2.19	2.22 ± .04	.11	-.50	-.03

significantly from the spacing calculated from the density according to the above formula. The measured spacing of forest trees (Table II), also agrees closely with the spacing calculated from the density according to the formula.

In populations in which frequency curves of the square roots of the measurements of spacing are strongly skewed either to the right or to the left, however, these formulas give answers which disagree considerably with the actual measurements of spacing. The expected mean spacing, calculated from their densities, for all kinds of plants listed in Table II depart considerably from the actual measurements of spacing taken by sextants. For those species whose individuals tend to be clumped in distribution, as shown by positive g_1 values, the measured spacings are less than the calculated ones. For the forest trees, however, which are somewhat more evenly distributed than random, as shown by a negative g_1 value, the spacing calculated from the density is less than the measured spacing. There is moreover, no close correlation between the g_1 value and the degree of difference between the expected spacing calculated from the density, and the actual measurements of spacing. Inasmuch as a large number of organisms in nature have nonrandom distributions, any general attempt to estimate spacing from population density, or the reverse, will evidently be impractical.

SPACING AS A MEASURE OF ASSOCIATION BETWEEN SPECIES

Several quantitative methods have been developed to measure the amount of association between 2 species (Forbes, 1907; Dice, 1945; Cole, 1949). These methods have been based on counts of the frequency of occurrence of the species being compared on sample plots or in samples of other kinds. The measures of association which are thus obtained have the disadvantage that they are gravely affected by the sizes of the samples (Nash, 1950). This difficulty could be in part avoided if we could base our comparisons on measurements of the spacing between the individuals of those pairs of species whose association is in question.

In order to develop such a method, let us assume that the members of a given species, alpha, are distributed over an area at random. Then, as pointed out above, the square roots of the distances between the individuals of this species, measured by sextants, will approach a normal curve. If now we add, also at random, an individual of another species, beta, and from this individual as a point of origin measure the distance to the nearest alpha individual in each surrounding sextant, then the square roots of these measurements will also form a normal curve. This will be true because the addition of another individual at random to the population will not change the random nature of the distribution. The only effect of adding the one individual of beta is to increase the previous population by one individual. Such an addition will decrease by a correspondingly slight amount the mean spacing between the individuals of the combined population. The square roots of the measurements, taken by sextants, of the spacing from any number of randomly distributed individuals of species beta, taken one at a time as points of origin,

to the nearest individuals of a randomly distributed species alpha, will consequently approach a normal curve.

Should one of the species of a pair whose association is being measured be considerably more abundant than the other species, then the measurements should always be made from the individuals of the rarer species. Should the individuals of the more abundant species be taken as points of origin for the measurements of spacing, no individual of the rarer species might happen to occur nearby. Under these conditions the frequencies of the square roots of the measurements might approach a normal curve, even though the rare species may actually be closely associated with the more abundant one.

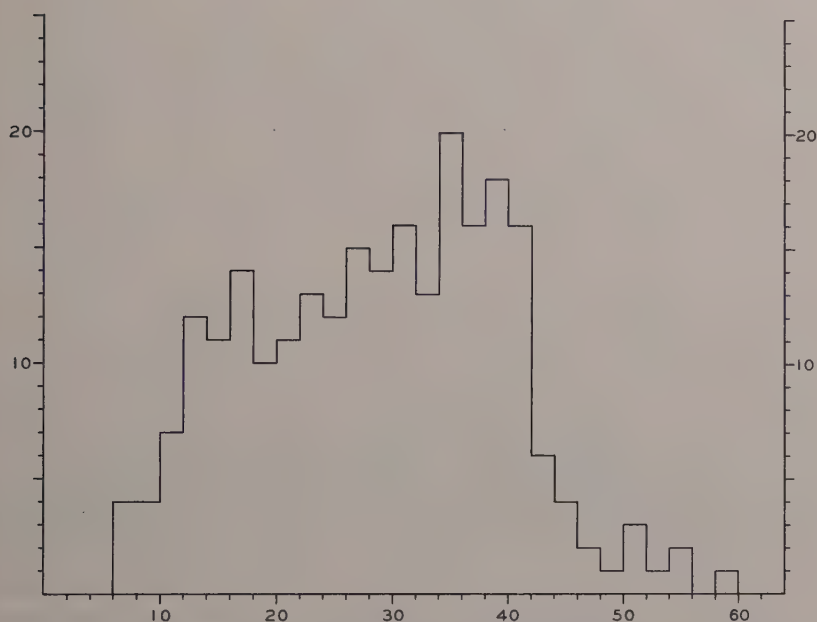


FIG. 12. Frequency polygon of square roots of distances from 50 individuals of *Solidago rigida*, taken as points of origin, to the nearest individual of *Liatris aspera* in each surrounding sextant. Measurements taken on chart constructed by Cain and Evans (1952) of the distribution of these plants over a grassy area on the Edwin S. George Reserve, Livingston County, Michigan.

As an application of the proposed method, I have measured the spacing between *Solidago* and *Liatris* on the plot on the George Reserve previously described. From the population of *Solidago* certain individuals were taken at random as points of origin for the first set of measurements. From each such point of origin, the distance in each surrounding sextant to the nearest individual of *Liatris* was measured. The square roots of these measurements form a nearly symmetrical frequency curve (Fig. 12) whose g_1 value is only an insignificant 0.02.

The curve, however, exhibits a moderate amount of negative kurtosis, the g_2 value being -0.59 , which is just below the 5 per cent level of significance (Table I). The top of the curve is noticeably plateau-like.

A similar result is obtained when we use individual plants of *Liatris* as the points of origin and measure to the nearest plants of *Solidago* in each surrounding sextant (Fig. 13). Again the g_1 statistic

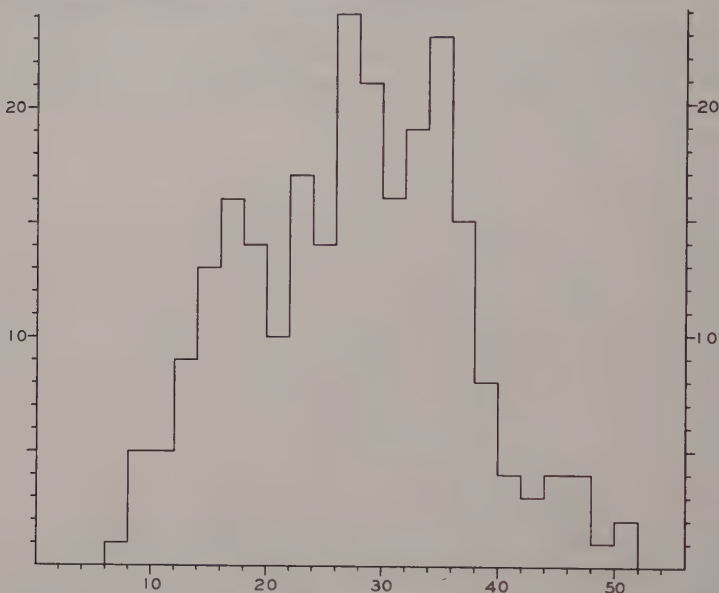


FIG. 13. Frequency polygon of square roots of distances from 50 individuals of *Liatris aspera*, taken as points of origin, to the nearest individual of *Solidago rigida* in each surrounding sextant. Measurements taken on a chart constructed by Cain and Evans (1952) of the distribution of these plants over a grassy area on the Edwin S. George Reserve, Livingston County, Michigan.

of the square roots of the measurements has only an insignificant value, indicating absence of skewness, but g_2 has again a negative value, this time, however, well below the 5 per cent level of significance (Table I).

I interpret the absence of skewness in the square roots of the measurements of the spacing between *Liatris* and *Solidago* to indicate the absence of any tendency toward either association or repulsion between the individuals of these 2 species. It will readily be agreed, however, that the association between a sufficient number of pairs of species has not as yet been measured by this method to be certain that absence of skewness will always indicate lack of association.

The significance of the departure from normality of the frequency curve of the square roots of the measurements by sextants of spacing between the individuals of 2 species can be tested by the g_1 statistic. Skewness to the left (g_1 positive) should indicate a tendency toward association between the 2 species, while skewness to the right (g_1 negative) should indicate repulsion. Unfortunately, I have at hand no example either of positive or negative skewness of the frequency curves of such interspecies measurements of spacing.

The presence of negative kurtosis in the frequency curves of the square roots of the distances from *Solidago* to *Liatris* and also from *Liatris* to *Solidago* is perhaps related to the fact that both these species are clumped in distribution. The points of origin for the measurements of spacing are consequently not taken completely at random, but also are clumped. In order to be sure whether this is a true explanation of the negative kurtosis in these frequency curves further studies will be needed. For the present I am assuming that this negative kurtosis does not indicate any tendency toward association or repulsion between the individuals of the 2 species

Another possible measure of association between 2 species might be presumed to be given by the expected spacing between them calculated from the density, compared with the actual measured spacing between the individuals. The measured mean spacing, however, both of *Solidago* to *Liatris* and of *Liatris* to *Solidago* departs seriously from the mean spacing calculated from the densities of these plants (Table II.) Perhaps this discrepancy is due to the negative kurtosis exhibited by the frequency curves of the interspecies measurements of spacing. Whatever the cause of the discrepancy, when one or both members of a pair of species are nonrandom in distribution, the expected mean spacing between them calculated from their density compared with the mean spacing obtained from actual measurements does not give a reliable measure of association.

Much more study will be needed to test the value of measures of interspecies spacing as an indicator of association or repulsion between the members of a pair of species. The scanty evidence at hand indicates that the g_1 statistic of measurements of interspecies spacing taken by sextants can be used as a test of the reliability of any tendency toward association or repulsion between the individuals. It is not anticipated, however, that g_1 or any other simple statistic can measure the strength of association between 2 given species. The individuals of 2 associated species may be related to one another in so many possible ways that no simple measure is likely to be adequate to describe every possible combination.

SUMMARY

For measuring the spacing between the individuals in any given population which is distributed over a single plane the following method is proposed: (1) A certain number of individuals in the population are taken at random as points of origin for the measurements. (2) From each such point of origin the distance is measured in each surrounding sextant to the nearest other individual in the same population. (3) The square roots of these measurements of spacing are treated statistically to derive means, variances, and other statistics.

The frequency curve of the square roots of the measurements of the spacing between individuals, taken according to the above described method, approaches normality when the distribution of the population is random. When the individuals are clumped, the curve is skewed toward the left. When the distribution is more even than random, the curve is

skewed toward the right. The significance of any irregularity of distribution may be evaluated by the g_1 and g_2 statistics. These statistics, moreover, give a measure of the degree of departure of any distribution from randomness.

The relations between mean population density per unit area (P) and the mean spacing between the individuals (S) measured by sextants should be given by the formulas: (1) $P = 1.155/S^2$ and (2) $S = \sqrt{1.155/P}$. These formulas seem to apply with fair precision when the distribution of the individuals in a population is approximately random or is more even than random, but they give erroneous values when the individuals occur in aggregations.

The square roots of the measurements of spacing between the individuals of one species, taken at random as points of origin, to the nearest individuals of another species in each surrounding sextant should approach a normal frequency curve when there is no association between the 2 species. The curve is expected to be skewed to the left when there is association between the members of the 2 species, or to the right when there is repulsion between them. The significance of any tendency toward association or repulsion can then be measured by the g_1 statistic. The frequency curves of the square roots of the measurements of the spacing between 2 species, each of which is clumped in distribution, however, exhibit negative kurtosis.

The measurement of spacing between individuals should be of general usefulness for describing the structure of populations and communities in quantitative terms. Its particular merit is that the measurements obtained are not affected by sample size.

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